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the kinds of which, like the varieties of mass-motion, are determined through localized imbibition. On this account, and because the motor acts have laid out the paths of growth, the parallelism between the series of morphological processes and of the motor processes is strikingly complete; but a presentation of these details, in the same order, must remain for the future.

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A SKETCH OF COMPARATIVE EMBRYOLOGY.

BY CHARLES SEDGWICK MINOT.

II.—THE FERTILIZATION OF THE OVUM.

IN the previous article we traced the relation of the genoblasts, or sexual products, to the cells from which they arise. We have now to consider the manner in which these products effect the creation of a new and complete animal. Now, the bodies of all animals are composed of cells and the productions of cells, hence to make an animal the first thing is to furnish cells. According to the theory propounded in the last article, an egg represents one part, a spermatozoön another part of a cell, hence a fusion of the two would again make a single perfect cell. This fusion actually occurs, and is called the impregnation or fertilization of the ovum.

Our knowledge of this phenomenon is extremely imperfect. It has, however, been the object of several important researches during the last few years, but we must wait for much more extended investigations before we can make any satisfactory generalizations. The following order of events is that which our present knowledge renders most probable—it must be remembered that we are dealing only with a probability. A *single* spermatozoön enters the egg and fuses with it. After the ejection of the polar globules, the nucleus of the egg is a small body which lies near the periphery, immediately underneath the globules. It then is called the *female pronucleus*, and travels—why or how is not known—towards the center of the egg, where it finally remains. A system of radiating lines runs out from it into the yolk, making, together with the pronucleus, the so-called female *aster*.

At some time during these changes, whether sooner or later perhaps does not matter, a single spermatozoön enters the egg. As the egg or yolk is surrounded by envelops, it is evident that either the spermatozoa must enter before the coverings are formed, or that it must have some way of passing them. For instance, in the hen the spermatozoa attain the yolk before the hard shell is formed in the oviduct. In other instances there is a special opening, often having a peculiar structure, which admits the passage of the spermatozoa, and is called the micropyle, Fig. 10. This opening is of course not an essential part of an egg, and merely permits the egg to be protected by an impermeable shell without excluding the spermatozoön. It is asserted that in some cases the micropyle is not a real opening, but only a permeable spot through which the spermotozoön can work its way (Kupffer).

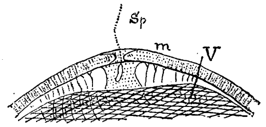

FIG. 10. — Spermatozoön entering the yolk of Petromyzon, the head having already traversed the micropyle; after Calberla.

It was stated above that only a single spermatozoön enters the yolk. The way in which the entrance of a second one is prevented is not definitely determined yet. It has, however, been stated by Fol and by Kupffer and Benecke that in the eggs observed by them (star-fish and lamprey) there is no vitelline membrane around the egg until after impregnation, when a complete envelop is rapidly formed by the yolk, effectually excluding all other spermatozoa. If this view is correct, then the egg has no proper cell membrane until after its fertilization; and all the coverings it has before that event, are only secreted around it by other cells, and not by itself.

When a spermatozoön penetrates into an egg, the head goes in first; after which the nucleus it contains loses its peculiar shape, transforming itself within the yolk into a small spherical or irregularly-shaped *male pronucleus.* The tail disappears—how is not known. This pronucleus, like the female, is surrounded by radiating lines, so that there is also a male *aster.* At this time the egg, as shown in Fig. 11, contains two pronuclei, and is still connected with the polar globules. The second pronucleus also travels towards the center of the egg, where the two pronuclei meet, both having meanwhile enlarged considerably. After coming in contact the two pronuclei fuse completely, making a single body, to which the very appropriate name of segmentation nucleus has been given. Possibly a contraction of the impregnated egg always occurs, either during or immediately after the entrance of the spermatozoön, so that a space intervenes between the yolk and the envelops of the egg. As little heed has been paid to this point, we are uncertain about it.

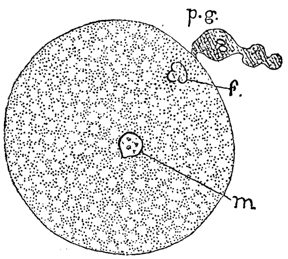

FIG. 11.—Egg of Nephelis three hours after laying. *m*, male,—*f*, female pronucleus; *p.g.*, polar globules; after Hertwig.

We thus have seen that a male and female element unite and make a single perfect cell. This fact offers a very strong support to the theory that cells contain two sexual constituents in a latent condition, and are therefore to be considered either hermaphroditic or sexless.

It has long been known that the egg of every animal must be impregnated by the spermatozoa of its own species, while on the other hand reproduction is dependent upon a certain dissimilarity, the existence of which is well established, although its nature cannot be even hypothetically explained. When the parents have been closely related for several generations, the sexual products alter in such a way that they cannot produce a complete animal by their fusion, although fusion with an element from another less closely related individual is still effectual. From these circumstances arises the necessity of cross breeding, a fact which has been so much discussed in public that I need not occupy further space to describe it. In a very few cases the genoblasts of nearly related species may unite efficiently, producing an animal partaking of the character of both parents—in short, a hybrid. Such exceptions are, however, extremely rare.

Since the offspring inherit the peculiarities of the parents, it is evident that the transmission must take place through the genoblasts, and various theories have been propounded to account for it, but no view has yet been brought forward which can justly be termed satisfactory, not even excepting the theory of pangenesis.

The formation of the impregnated egg, with its segmentation nucleus, marks the beginning of new cycle of life, for the cell so formed is endowed with a mysterious and remarkable power, which entirely distinguishes it from almost every other kind of cell known at present. The fertilized ovum is charged with forces which cause it to divide into numerous cells, and cause these cells to arrange themselves upon the model of the parents which formed the egg and spermatozoa, and to imitate the peculiarities of the cells in each locality, making an eye where the parent had an eye, a gland where the parent had a gland—only the imitation is imperfect, the offspring is not absolutely the same as the parent. Evidently the fusion of the genoblast is the source of an increased vitality and of a formative power which is specific in each case, *i. e.*, the action and result of which is predetermined.

This marvelous formative power has always excited the interest and astonishment of naturalists. It is one of the fundamental distinctions of life, since no similar power occurs in inorganic nature. It is important to note, therefore, that it must enter into all cells, otherwise some of them would not form in the right place and manner. That other cells than the fertilized ovum contain such a power is shown by the formation of buds and strobila, and more strikingly by the development of *pseudova.* In the latter instance, the development begins with a cell arising in the ovary, and which resembles an ordinary egg very closely. Such cells are formed in various animals, notably in the plant lice, but, although they are so like eggs, the pseudova differ by being capable of developing into a complete animal without impregnation.

For want of space, it is impossible to describe the formation of buds and strobila, let it therefore suffice to say, that the reproduction depends in both cases upon the separation of a *cluster* of cells (instead of a single cell or pseudovum) from the body of the parent. This cluster grows up into a complete animal, in which the structure of the parent, or sometimes of the grandparent, is imitated by the action of the formative force of the cluster of cells. Hence it is evident that a similar power is bestowed upon several cells, which is the thesis we started to prove.

III.—SEGMENTATION AND THE FORMATION OF THE GASTRULA.

After the impregnation has been completed, and the two pronuclei have fused, to form the segmentation-nucleus, there usually follows a period of quiescence, during which no visible changes occur. It is not known whether such a period is always intercalated in the course of development; but it has been observed frequently. After this pause the process of segmentation begins, which has for its essential purpose the multiplication of cells; the further history of the egg is a description of the way in which the cells, constantly on the increase, arrange themselves in definite order, until they have gradually created, or, more truly, become, the adult animal. The object of embryology is to discover the laws according to which this arrangement is developed.

We, of necessity, begin with a study of the process of segmentation; but the details are so numerous that we can indicate only a few of them. The first result is the formation of two sets of cells. In one set the cells are small; in the other set they are large. Except in the sponges, the small cells form the outside covering of the body, appearing as a sac, or vesicle. The large cells form the lining of the digestive canal, or primitive stomach, and are, therefore, enclosed in the outer vesicle made by the small cells. It appears that this disposition arises in two entirely distinct ways. First, the cells formed by segmentation arrange themselves in the shape of a sphere, hollow inside, and its walls consisting of a continuous layer of cells. One half is composed of small cells; the other half of large cells. Second, the result of segmentation is likewise a hollow sphere, but with double walls; the outer wall of small cells, the inner wall of large cells. In both cases the sphere transforms itself into a so-called *gastrula*. In the first instance, the large cells become inverted inwards, or, in technical language, invaginated; while the small cells grow down and around the others, until they encase them, leaving only a small opening, the primitive mouth. In the second instance, an opening breaks through both walls, thus making a mouth. This method of development is much rarer than the other, and unfortunately has never been studied in a thoroughly satisfactory manner.

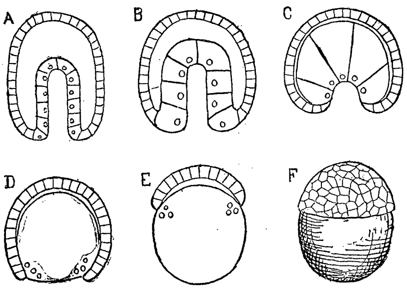

FIG. 12.—Diagrams of the principal modifications of the Gastrula. *cf.* Text. *A–E* represent sections.

The accompanying figure displays diagrammatically the principal forms of gastrulæ. *A* is a very simple form, such as occurs among Echinoderms. The difference in size between the two sets of cells is slight, but evident. In *B*, the difference is more marked, and fairly represents a gastrula of *Amphioxus*. In *C*, the difference is very great, and corresponds to a form observed in certain Gasteropods. In *D*, the inner set is no longer separated into distinct cells, although there are a number of nuclei, each of which marks the center of a future cell. In such an instance we should regard the whole inner set as a nutritive yolk, not yet transformed into a definite cell-layer. This figure is particularly instructive, because it shows that what we call the yolk is not something distinct from the germ, but really belongs to the inner layer of the embryo. *E* shows a similar egg, in which the outer set of cells has not yet grown around the yolk. This outer layer was called by the earlier embryologists the blastoderm, in all those eggs with a great deal of yolk. *F* shows the same egg not in section, but seen from the outer surface, to exhibit the cap of small cells, or the blastoderm, resting upon the large yolk. Those eggs in which the difference in size between the two sets of cells is not excessive (A–C) are called *holoblastic*, while those in which the yolk remains more or less intact for a considerable time (D–F) are termed *meroblastic*.

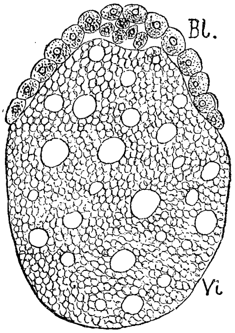

FIG. 13.—Formation of the blastoderm in *Oniscus murarius*, after Bobretzky.

In order more fully to illustrate the peculiarities of the process of segmentation, it is necessary to consider the holoblastic eggs further. Fig. 13 represents an actual section of an egg of the sow-bug, *Oniscus*, after Bobretzky, corresponding very nearly to the diagram *E*, of Fig. 12. Fig. 14 is a similar section through the egg of a moth (*Pieris crataegi*), and shows a number of nuclei, each surrounded by a little mass of protoplasm, and scattered irregularly through the yolk. Their number gradually increases, and each one becomes the center of a distinct cell. This is merely a peculiar modification of the ordinary method of cell division into two equal parts, for in the moths and butterflies and some other animals the large yolk divides gradually, by forming several nuclei, and so breaking up into a considerable number of cells piled up one over the other. We shall have oc-

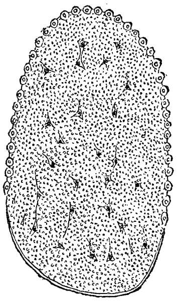

FIG. 14. — Section of a segmenting egg of a moth; after Bobretzky.

casion to recur to this matter in speaking of the development of vertebrates.

The embryology of sponges is important because they do not have any gastrula. It will be described in our next article. Except in the sponges, the small cells form the outside layer and are called the *ectoderm*, while the large cells form the inside layer, or *entoderm*. In England the attempt has been made to substitute epiblast for ectoderm, and hypoblast for entoderm, but the change seems to me useless and confusing. In face of the present tendency to substitute new and difficult for old and simple names every protest is desirable. Compounding English polysyllables from Latin and Greek confers, in most cases, no benefit to science. The coining of such terms ought to be restricted in its application to things which have no accepted name and for which no straightforward English term can be found.

The next progress after the formation of the ectoderm and entoderm does not occur among all animals, but only in those above the Cœlenterates. I refer to the development of a distinct middle layer of cells, the *mesoderm*, situated as shown in Fig. 15, between the two primitive layers. Of the origin and characteristics of the mesoderm I shall treat in the next article.

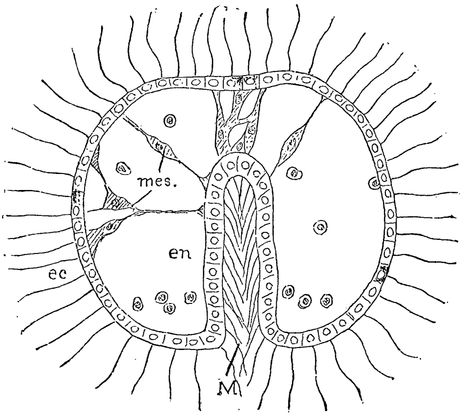

FIG. 15.—Section of a gastrula of *Toxopneustes lividus*, after Selenka; *mes.* mesoderm.

A great many embryos live in the water, and have the power of locomotion long before they have any muscles. For this purpose the ectoderm in these forms is provided with cilia or vibratile hairs, which may be longer (Fig. 15) or shorter. In most free embryos, moving by cilia, we find distinct bands, along which the cilia are more developed and powerful; as the ciliated bands are often pigmented, while the rest of the embryo is transparent or light-colored, they are very conspicuous. We shall have to recur to them.

The authorities for the general views advanced above are the discussions in a long series of special papers. Prof. Haeckel[1] has written a great deal upon the gastrula and its significance, and has published several popular works on embryology. Unfortunately, he is inaccurate and untrustworthy to a degree surpassing any other scientific writer I can recall, for on almost every page are mistakes it requires little knowledge to detect. He is, therefore, utterly useless to the beginner. I mention this, not alone as my personal conviction, but also as the judgment of competent and distinguished critics, some of whom are even more severe in their condemnation. For these considerations I shall not quote Haeckel as an authority. The references to some of the special papers I have consulted will be given hereafter.

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[1] "Professor Haeckel's principal articles on the Gastrula are to be found in the *Jena Zeitschrift für Naturwissenschaften*, Band. VIII, p. 1, and *Biologische Studien*, 2tes Heft. 1877. Haeckel introduced the term *Gastrula*, and his writings and speculations have afforded a powerful stimulus to embryological research."